

## VARIATION IN FORAGING BEHAVIOR AND BODY MASS IN BROODS OF EMPEROR GEESE (*CHEN CANAGICA*): EVIDENCE FOR INTERSPECIFIC DENSITY DEPENDENCE

JOEL A. SCHMUTZ<sup>1,3</sup> AND KAREN K. LAING<sup>2,4</sup>

<sup>1</sup>U.S. Geological Survey, Alaska Biological Science Center, 1011 East Tudor Road, Anchorage, Alaska 99503, USA; and

<sup>2</sup>Department of Wildlife and Fisheries Biology, University of California, Davis, California 95616, USA

**ABSTRACT.**—Broods of geese spend time feeding according to availability and quality of food plants, subject to inherent foraging and digestive constraints. We studied behavioral patterns of broods of Emperor Geese (*Chen canagica*) on the Yukon–Kuskokwim Delta, Alaska, and examined how feeding and alert behavior varied in relation to habitat and goose density. During 1994–1996, time spent feeding by Emperor Goose goslings and adult females was positively related to multispecies goose densities near observation blinds, and not to just Emperor Goose density. Similarly, body mass of Emperor Goose goslings was more strongly related (negatively) to multispecies goose densities than intraspecific densities. A grazing experiment in 1995 indicated that most above ground primary production by *Carex subspathacea*, a preferred food plant, was consumed by grazing geese. Those results demonstrate that interspecific competition for food occurred, with greatest support for goslings whose behavioral repertoire is limited primarily to feeding, digesting, and resting. Although the more abundant Cackling Canada Geese (*Branta canadensis minima*) differed from Emperor Geese in their preferred use of habitats during brooding rearing (Schmutz 2001), the two species occurred in equal abundance in habitats preferred by Emperor Goose broods. Thus, Cackling Canada Geese were a numerically significant competitor with Emperor Geese. Comparing these results to an earlier study, time spent feeding by goslings, adult females, and adult males were greater during 1993–1996 than during 1985–1986. During the interval between those studies, densities of Cackling Canada Geese increased two to three times whereas Emperor Goose numbers remained approximately stable, which implies that interspecific competition affected foraging behavior over a long time period. These density-dependent changes in foraging behavior and body mass indicate that interspecific competition affects nutrient acquisition and gosling growth, which has a demonstrated effect (Schmutz 1993) on juvenile survival of Emperor Geese. Management of Emperor Geese should consider interspecific relations and densities of all goose species occurring on the Yukon–Kuskokwim Delta, Alaska. Received 9 October 2001, accepted 17 July 2002.

**RESUMEN.**—El tiempo que las crías de gansos utilizan para alimentarse depende de la disponibilidad y calidad de las plantas de las cuales se alimentan, y está sujeto a las restricciones inherentes del forrajeo y la digestión. Estudiamos los patrones conductuales de crías de *Chen canagica* en el Delta Yukon–Kuskokwim, Alaska, y examinamos cómo la conducta de alimentación y de alerta variaron con respecto al hábitat y densidad de gansos. Durante 1994–1996, el tiempo que los gansos juveniles y las hembras adultas gastaron en la alimentación, se relacionó positivamente con las densidad de gansos de múltiples especies que se encontraban cerca de los puestos de observación, y no sólo con las densidades de *C. canagica*. Similarmente, el peso corporal de los juveniles de *C. canagica* estuvo más relacionado (negativamente) con las densidades de gansos de múltiples especies que con las densidades intraespecíficas. Un experimento de pastoreo en 1995 indicó que la mayoría de la producción primaria de *Carex subspathacea* existente por sobre el suelo, una planta preferida como alimento, fue consumida por los gansos que pastoreaban. Estos resultados demuestran que ocurrió competencia interespecífica por el alimento, lo que fue mejor apoyado por las conductas de los gansos juveniles cuyo repertorio conductual está principalmente limitado a alimentarse, digerir y descansar. Aunque el ganso *Branta canadensis minima* (más abundante)

<sup>3</sup> E-mail: joel.schmutz@usgs.gov

<sup>4</sup> Present address: U.S. Fish and Wildlife Service, 1011 East Tudor Road, Anchorage, Alaska 99503, USA.

difirió de *C. canagica* en las preferencias de uso de hábitats durante el período de cría (Schmutz 2001), las dos especies ocurrieron en la misma abundancia en los hábitats preferidos por las crías de *C. canagica*. Así, *B. canadensis minima* fue un competidor numéricamente significativo para *C. canagica*. Comparando nuestros resultados con los de un estudio anterior, el tiempo invertido en la alimentación por los juveniles, hembras adultas y machos adultos fue mayor durante 1993–1996 que durante 1985–1986. Durante el intervalo de tiempo entre estos estudios, las densidades de *B. canadensis* mínimos aumentaron dos a tres veces mientras que los números de *C. canagica* permanecieron aproximadamente estables, lo que implica que la competencia interespecífica afectó la conducta de forrajeo por un largo período de tiempo. Estos cambios denso-dependientes en la conducta de forrajeo y peso corporal indican que la competencia interespecífica afecta la adquisición de nutrientes y el crecimiento de los juveniles, lo que tiene un efecto demostrado (Schmutz 1993) en la supervivencia de juveniles de *C. canagica*. El manejo de los gansos *C. canagica* debe considerar las relaciones interespecíficas y densidades de todas las especies de gansos que ocurren en el Delta Yukon–Kuskokwim, Alaska.

RECRUITMENT TO BREEDING populations of geese is strongly affected by environmental conditions experienced by broods before fledging (Cooch et al. 1989, Williams et al. 1993, Sedinger et al. 1995a). Geese are highly selective herbivores (Sedinger 1997), and growth rates of goslings are sensitive to changes in the quality and quantity of food plants (Lindholm et al. 1994, Gadallah and Jefferies 1995, Sedinger et al. 1997, LePage et al. 1998). Reduced nutrient availability and gosling growth rates have demographic consequences because small juvenile body size markedly affects subsequent survival and fecundity (Owen and Black 1989, Schmutz 1993, Sedinger et al. 1995a, van der Jeugd and Larsson 1998). When confronted with low abundance or quality of food, geese compensate by increasing time devoted to foraging (Sedinger and Raveling 1988, Mulder et al. 1995, Hupp and Robertson 1998). For goslings, such behavioral compensation may ultimately be limited by processing constraints (Sedinger and Raveling 1988), at which point growth rates decline. For adults, increased time spent feeding necessitates a reduction in one or more other behaviors and may influence the time devoted to protecting their young (Williams et al. 1994).

Emperor Geese (*Chen canagica*) are the least abundant of four species of geese that nest and rear broods sympatrically on the Yukon–Kuskokwim Delta (King and Derksen 1986, Sedinger 1996a). Black Brant (*Branta bernicla nigricans*), Cackling Canada Geese (*B. canadensis minima*), Greater White-fronted Geese (*Anser albifrons*), and Emperor Geese all declined in numbers from the late 1960s to mid-1980s. Since then, numbers of Cackling Canada Geese

and Greater White-fronted Geese have increased steadily at >10% per annum (Bowman et al. 1999). Black Brant are the sole colonial nesting goose on the Yukon–Kuskokwim Delta, with dynamics differing among colonies and some colonies increasing recently (Sedinger et al. 1993, 1998). In contrast, numbers of Emperor Geese have remained stable since the mid-1980s at a depressed level compared to previous counts (Petersen et al. 1994, Bowman et al. 1999). Such changes in goose abundance provide an important environmental context for how broods may exploit resources.

Previous studies of other goose species during brood rearing have found that intraspecific densities were correlated with behaviors (principally feeding; Sedinger et al. 1995b, Fowler and Ely 1997) and with concomitant effects on juvenile demographics (growth and early survival; Sedinger et al. 1995a, 1998). However, no studies have explicitly examined how multiple, sympatric species of geese may compete for food and how such competition may be manifested in behavior and demography. Ecological theory predicts that in stable ecosystems, sympatric species will be in equilibria if they have evolved divergent patterns of use of limited resources (Wiens 1989). However, equilibria is rarely expected for goose populations because land-use patterns and harvest management continually perturb populations from such stability (Ankney 1996, Schmutz and Ely 1999, Menu et al. 2002). Further, if during temporary periods of allopatry (e.g. nonbreeding seasons), goose species are differentially affected by demographically important perturbations, then conditions may arise for asymmetrical competition during summer periods of sympatry.

Asymmetries in competitive ability produced by changing ecological conditions has led to the endangerment of populations and species (Tanner et al. 1994, Bardsley and Beebee 2001).

We examined whether Emperor Geese are subject to interspecific competition during the environmentally sensitive brood-rearing period. Specifically, we used observations of broods during 1993–1996 to test the hypotheses that time spent feeding by Emperor Geese and the mass attained by growing goslings were a function of goose density. To explicitly test whether interspecific competition was relevant, we compared models of brood behavior and gosling body mass that included densities of Emperor Geese with those that included the collective density of Emperor Geese, Cackling Canada Geese, and Black Brant. We compared our data to behavioral data from 1985–1986 and body mass and goose density data from 1990 to suggest there has been a long-term progressive increase in competition among goose species on the Yukon–Kuskokwim Delta.

#### STUDY AREA AND METHODS

We studied behavior of Emperor Goose broods during 1993–1996 near the Manokinak River on the Yukon–Kuskokwim Delta, Alaska. Plant communities in the vicinity of observation blinds were dominated by two adjacent, halophytic communities. The more inland and expansive community was a nearly monospecific meadow of *Carex ramenskii*. This community is termed Brackish Fringe Wet Sedge Meadow by Jorgenson (2000). Progressing down in elevation towards tidal waters, there was an abrupt border between *C. ramenskii* meadows and the much shorter, lawn-like community dominated by *C. subspathacea*, termed Brackish Fringe Wet Graminoid Meadow by Jorgenson (2000). That vegetation occurred in a strip along the border with *C. ramenskii* meadows as well as in small, dispersed patches among otherwise primarily barren mudflat. When geese were in that plant community dominated by *C. subspathacea* or in barren mudflat, we recorded them as being in *C. subspathacea*. Overall, *C. ramenskii* was much more abundant than *C. subspathacea* (Jorgenson 2000). Emperor Geese selectively used *C. ramenskii* and *C. subspathacea* habitats, relative to others (Schmutz 2001), and our observation blinds were subjectively located at the border between those habitats to maximize numbers of geese observed.

**Brood observations.**—We observed broods of Emperor Geese from a series of 10 elevated blinds distributed across a 70 km<sup>2</sup> area. We observed broods from a few days after peak hatch of goslings to ~10

days before fledging, an approximate four week period each year. To minimize human-induced alteration of behavior, observers stayed in blinds for two days at a time and no behavior samples were collected during the first 3 h of each session in a blind.

A single observation consisted of watching a focal brood for 40–60 min, and each minute recording the instantaneous behavior and habitat of each individual. Those observations were distributed throughout diurnal periods. Broods were selected by randomizing which window of the blind we peered from and choosing the first brood we saw that was within ~400 m. Behaviors were recorded according to the following categories: feeding, alert, travel, resting, and maintenance. A missing category was also used if broods temporarily disappeared from view. Observations were discontinued if adults disappeared from view for more than 5 min. “Feeding” was defined as actively grabbing or chewing plants or searching for the next bite with the head held below horizontal. “Alert” was any posture with the head and neck held in an extended and apparently attentive state while either sitting or standing. “Travel” was primarily walking, where broods were moving but not actually engaged in feeding. “Resting” was when geese were stationary and not alert nor feeding. “Maintenance” behaviors included preening, bathing, and drinking. During each 1 h sample, we also recorded the presence or absence of Arctic fox (*Alopex lagopus*), aircraft, alertness directed towards Glaucous Gulls (*Larus hyperboreus*), or aggressive interactions with other goose broods.

We identified sex of adults by observing brooding behavior (only done by adult females), reading neck collars or tarsal bands worn by a subset of geese (Schmutz and Morse 2000), or by comparing within pairs the degree of staining of the otherwise white head and neck plumage. Those feathers are stained orange during hyperphagic foraging shortly after arrival on the breeding area, and within pairs, the staining is darker for females than males due to greater spring feeding activity by females (Petersen et al. 1994; M. Petersen unpubl. data). We omitted data for those few broods where sex classification of adults was ambiguous. Goslings were not individually identifiable, so we recorded the behavior displayed by the majority of the brood at each instantaneous sample.

We treated each brood observation as an independent sample. Some broods with banded adults were sampled more than once, so we randomly selected one observation per banded brood for inclusion in analyses presented here. The probability of repeated sampling of unidentifiable (not banded) broods was low because of the high number of such broods relative to banded broods (Sedinger and Raveling 1990) and our spatial distribution of sampling among 10 blinds.

*Descriptive analysis of behavior.*—One of our objectives was to quantitatively describe the behavioral time budget of broods so that we could assess whether those behaviors varied among years in our study and whether they differed from that of Laing's (1991) previous study. This analysis concerns data collected during 1993–1996, whereas tests of density effects on behavior (below) is for 1994–1996. In 1993, the necessary density data were not collected.

We made an *a priori* decision to analyze goslings, adult females, and adult males separately. Explicit testing for differences seemed unnecessary because many studies have documented marked differences in behavior among these classes of geese (Sedinger and Raveling 1990, Sedinger et al. 1995b, Fowler and Ely 1997). Similarly, several studies of goose behavior have found time of day to be an unimportant factor (Laing 1991, Sedinger et al. 1995b, Fowler and Ely 1997). We corroborated such findings for our data during preliminary analyses and do not consider that factor further. We also omitted from analysis the infrequent observations of pairs that had no young.

Prior to analysis, we applied arcsine transformations to all percentage data to better meet the distributional assumptions of linear models (Sokal and Rohlf 1981). We treated year as a categorical main effect and brood size and date as continuous covariates in a multivariate analysis of covariance (MANCOVA). We included brood size and date because some studies have found they affect brood behavior (Loonen et al. 1999, Sedinger et al. 1995b, Williams et al. 1994). When the overall model *F*-test indicated a significant effect, we used univariate ANCOVA to assess importance of the three covariates on each behavior. Least-squares estimates of mean behaviors for each year are presented to account for the effects of the covariates.

*Goose density counts.*—Two indices of local goose density were collected from observation blinds. Those two indices were combined (in a process described below) to produce density estimates for each species for each observation blind in each year, which was necessary for testing the effects of goose density on behavior. The first of those two indices was obtained by counting, once per day, the number of Emperor Goose broods in which all goslings could be observed. That is referred to as a "peak count", and the timing of that count within a day was subjectively determined to maximize numbers of broods simultaneously seen. The second density index was obtained by counting, every 2 h, the numbers of broods (irrespective of whether all goslings were visible) of each goose species that were within the boundaries of a plot or plots within ~250 m of each observation blind and delineated with wood lathe. Those plots contained approximately equal amounts of *C. ramenskii* and *C. subspathacea* habitat. Few Greater White-fronted Geese were seen in these plots (<3% of counts) and are not considered further.

Those counts are referred to as "relative density counts" because their primary purpose was to observe enough Emperor Geese, Cackling Canada Geese, and Black Brant in a defined area to provide an estimate of the relative density of the three species around our observation blinds. We enlarged plots multiple times during the study to obtain larger samples and exact plot dimensions were not measured. Therefore, those counts only indicated the local density of Emperor Geese relative to Cackling Canada Geese and Black Brant, and they do not by themselves address changes in a single species' density over time (years). During those counts, we also made instantaneous assessments of the dominant habitat and behavior for each brood of each species.

Peak and relative density counts were combined to arrive at density estimates for each species in each year at each blind. That was done by first using peak counts of Emperor Geese in an ANCOVA model to produce least-squares estimates of numbers of Emperor Geese for each blind location and year, after controlling for the covariate date. Relative density counts were then used to adjust peak counts to reflect numbers of geese of multiple species. For example, from the relative density counts we formed a ratio of the number of Cackling Canada Geese over the number of Emperor Geese for each blind and year, and multiplied that ratio by the mean peak count for the corresponding blind and year. By then adding that product to the peak count, we arrived at a measure of combined Emperor and Cackling Canada goose density that could be appropriately compared to that of Emperor Geese alone. We used a similar process to also calculate blind- and year-specific estimates of the combined density of Emperor Geese, Cackling Canada Geese, and Black Brant. Thus, we had three different density variables to use in subsequent analyses of behavior—one representing an intraspecific effect (Emperor Goose density) and two versions of interspecific effects (combined Emperor and Cackling Canada goose density, and combined Emperor Goose, Cackling Canada Goose, and Black Brant density).

*Testing effects of goose density and habitat on behavior.*—We focused these analyses on the two most prevalent behaviors—feeding and alert. We used the same data and a similar series of ANCOVA models as that described above for the descriptive analysis of behavior, except precluded to 1994–1996 because of the omission of density and habitat data in 1993. Six sets of ANCOVA were conducted (two behaviors for each of three age-sex classes). The descriptive analysis led us to include date but not brood size as a covariate in those models. We first evaluated whether habitat (*C. ramenskii* vs. *C. subspathacea*) and date were important factors affecting behavior by comparing the relative fit of models (as judged by the Akaike information criterion [AIC]; Burnham and Anderson 1998) with and without those factors in-

cluded in the model structure. The importance of a factor (covariate) can be judged by its inclusion in the best (parsimonious) model, which is identified by the lowest AIC value (Burnham and Anderson 1998). We then used that parsimonious model, with respect to habitat and date, and constructed a set of four models to test the effect of goose density on behavior. Those four models were as follows: a model that included no goose density term; a model with a density term reflecting just Emperor Goose density (an intraspecific effect); a model with a term reflecting the combined density of Emperor and Cackling Canada Geese (one type of interspecific effect); and a model with a term reflecting the combined density of Emperor Geese, Cackling Canada Geese, and Black Brant (a second type of interspecific effect). Akaike information criterion was then used to infer which model best fit the data and thus draw conclusions about the effect of goose density on behavior. An AIC weight was also calculated for each model, where the set of weights sum to 1.0 and each model's weight intuitively quantifies the strength of evidence that the model is the best fit to the data (Anderson et al. 2000).

Once a parsimonious model had been selected to describe the effects of habitat, goose density, and date, we then constructed two additional models to examine the effects of disturbance. Those models each included a dummy variable that represented occurrence of either gull or aircraft disturbance during a given time budget sample. We then evaluated whether inclusion of a disturbance term further reduced the AIC. We used a similar modeling approach to evaluate whether the time spent in *C. ramenskii* versus *C. subspathacea* habitats varied with date.

*Gosling body mass relative to densities.*—We captured flocks of geese when goslings were approximately six weeks old and parents had molted their primaries and were flightless. Flocks were captured throughout the study area, all geese were banded, and systematic subsamples (e.g. every third bird) were weighed. As growth of goslings is approximately linear at that age (Sedinger 1996b), we regressed body mass against capture date within each year to adjust body mass to a mean date of six weeks after peak hatch of geese. Body-mass data were obtained in 1990 in an earlier study at that site (Schmutz 1993) and in 1993–1996. Our brood-density data in 1994–1996 allowed us to explicitly examine whether variation in body mass among years was related to intra- or interspecific goose densities. Densities of geese among blinds were summed within each year and five linear regression models were fit to the body mass data: a year effect, an intraspecific density effect, two versions of interspecific density effects (similar to described previously), and a null model of no factor accounting for variation in body

mass. Fit of those models was then compared with AIC values.

Brood density data were not collected in 1990 or 1993. However, nest density data were collected for all goose species in 1990 and again in 1997. Seven 0.32 km<sup>2</sup> plots were distributed across the study area and intensively searched during incubation. Numbers of nests for each species were tallied.

*Grazing effects on Carex subspathacea.*—In 1995, a grazing experiment was conducted in strips of *C. subspathacea* near one of the observation blinds used in this study. The objective was to document apparent offtake (Person et al. 1998) of plant biomass by grazing geese during the brood-rearing period. During hatch of goslings, eight sets of three 0.1 m<sup>2</sup> plots were established. Those eight sets were placed in an approximately linear fashion, parallel to the river course and the interface of the *C. ramenskii* and *C. subspathacea* habitats described above. This pattern corresponded to the linear distribution of *C. subspathacea*, and each set of plots was ~150 m from an adjacent set(s) of plots. Each plot was measured for above ground biomass of *C. subspathacea* (by clipping and weighing all vegetation), and within each set of three plots, we randomly selected the treatment (time of sampling) each received. One plot was sampled immediately to represent biomass available at peak hatch of goslings, and the other two plots were sampled 30 days later, near the end of the brood-rearing period. One of those latter two plots within each set was randomly chosen to be enclosed within a wire mesh fence for this 30 day period, and thus unavailable to grazing by geese. The difference in biomass of those two plots sampled at 30 days provides a measure of biomass consumed by geese, and by comparison to enclosed plot biomass, a measure of what percentage of above ground primary production is consumed (McNaughton et al. 1996, Person et al. 1998). Means and confidence intervals of biomass for the three types of plots were compared (Johnson 1999).

## RESULTS

We obtained 137, 143, 74, and 66 time-budget samples from Emperor Goose broods during 1993–1996. Behavior of goslings, adult females, and adult males varied in relation to year and date ( $P < 0.027$  for each MANCOVA). However, behavior appeared unrelated to brood size ( $P = 0.239$  for goslings,  $P = 0.097$  for adult females, and  $P = 0.150$  for adult males). We then further investigated the potential for a brood size effect for adult females by examining the ANCOVA for each behavior. Only time spent resting or missing was related to brood size. Females with large broods appeared to rest more



TABLE 1. Mean percentage of time ( $\pm$  SE) spent in various behaviors by broods of Emperor Geese. We sampled focal broods for 1 h periods during which instantaneous assessments of behavior were recorded each minute. We present least-squares means, controlling for date effects.

Age/sex	Year	Behavior						
		Feed	Alert	Main-tenance	Brooding	Travel	Rest	Missing
Adult female	1993	59 $\pm$ 2.2	10 $\pm$ 0.9	5 $\pm$ 0.6	4 $\pm$ 1.1	9 $\pm$ 0.7	9 $\pm$ 1.2	5 $\pm$ 0.6
	1994	63 $\pm$ 2.1	9 $\pm$ 0.9	3 $\pm$ 0.6	6 $\pm$ 1.1	10 $\pm$ 0.7	5 $\pm$ 1.2	5 $\pm$ 0.6
	1995	54 $\pm$ 3.0	14 $\pm$ 1.2	3 $\pm$ 0.8	4 $\pm$ 1.5	8 $\pm$ 1.0	13 $\pm$ 1.6	6 $\pm$ 0.9
	1996	55 $\pm$ 3.2	16 $\pm$ 1.3	2 $\pm$ 0.8	4 $\pm$ 1.7	8 $\pm$ 1.0	10 $\pm$ 1.8	6 $\pm$ 0.9
Adult male	1993	42 $\pm$ 1.9	29 $\pm$ 1.5	4 $\pm$ 0.5	0	11 $\pm$ 0.8	11 $\pm$ 1.3	5 $\pm$ 0.8
	1994	43 $\pm$ 1.9	29 $\pm$ 1.5	4 $\pm$ 0.5	0	12 $\pm$ 0.8	9 $\pm$ 1.3	4 $\pm$ 0.8
	1995	37 $\pm$ 2.6	32 $\pm$ 2.0	4 $\pm$ 0.7	0	10 $\pm$ 1.1	14 $\pm$ 1.8	5 $\pm$ 1.1
	1996	36 $\pm$ 2.8	43 $\pm$ 2.2	4 $\pm$ 0.8	0	8 $\pm$ 1.1	7 $\pm$ 1.9	3 $\pm$ 1.2
Gosling	1993	68 $\pm$ 2.8	1 $\pm$ 0.7	2 $\pm$ 0.3	3 $\pm$ 1.1	6 $\pm$ 0.6	8 $\pm$ 1.0	17 $\pm$ 1.9
	1994	73 $\pm$ 2.7	1 $\pm$ 0.7	1 $\pm$ 0.2	6 $\pm$ 1.1	7 $\pm$ 0.6	3 $\pm$ 0.9	14 $\pm$ 1.9
	1995	63 $\pm$ 3.8	0 $\pm$ 0.9	1 $\pm$ 0.3	5 $\pm$ 1.5	6 $\pm$ 0.8	4 $\pm$ 1.3	26 $\pm$ 2.6
	1996	67 $\pm$ 4.0	0 $\pm$ 1.0	1 $\pm$ 0.4	6 $\pm$ 1.6	7 $\pm$ 0.9	5 $\pm$ 1.4	18 $\pm$ 2.8

( $\beta_{\text{rest}} = 0.97$ , SE = 0.45,  $P = 0.003$ ) and be missing less ( $\beta_{\text{miss}} = -0.45$ , SE = 0.23,  $P = 0.049$ ) than females with small broods. Because broods were least observable while resting due to their lower profile and the tall vegetation used for resting, we suspect that large broods were simply easier to see and that most of the actual behavior exhibited while missing was resting. Feeding and alert behaviors dominated

the time-budget of adult geese (Table 1). For adult females, neither feeding ( $\beta_{\text{feed}} = -0.75$ , SE = 0.82,  $P = 0.357$ ) nor alert behavior ( $\beta_{\text{alert}} = 0.12$ , SE = 0.33,  $P = 0.72$ ) was related to brood size. It was therefore concluded that no effect of brood size on behavior of adults or goslings could be detected. Least-squares means were then estimated for each behavior for each year, adjusting for date (Table 1). Across the four years of our study, time spent feeding by broods was greater than that spent by broods during Laing's (1991) earlier study in 1985–1986 (Fig. 1).

*Goose density.*—Least-squares means of peak counts of Emperor Goose broods visible during 1994–1996 from a single tower ranged from 4 to 19 broods. Mean ratio of the number of Cackling Canada Geese to Emperor Geese during relative density counts was 1.02, and mean ratio of Cackling Canada Geese and Black Brant to Emperor Geese was 1.43. Estimated means of total goose density per tower (all three species combined) ranged from 8 to 38 broods. While in plots around blinds, Black Brant used *C. subspathacea* habitats more than Emperor Geese and Cackling Canada Geese, and Black Brant spent less time in *C. ramenskii* habitats feeding than the other two species (Table 2). For data from relative density counts, the mean CV across towers and years for Emperor Geese was 130 (95% CI = 104–157), whereas the respective mean CV for Cackling Canada Geese and Black Brant were 183 (151–214) and 291 (233–349), thus indicating that Emperor Geese were more

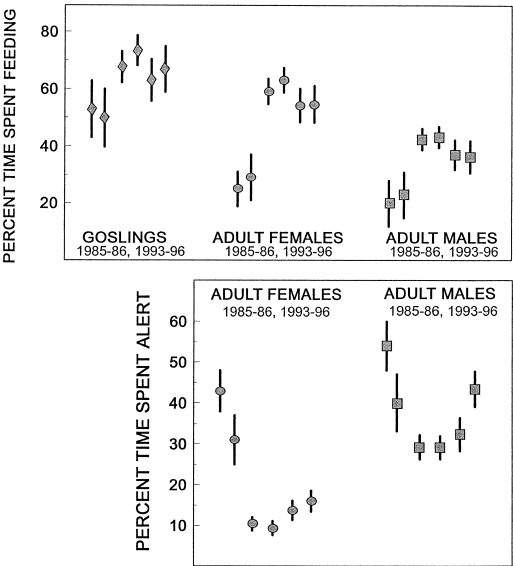


FIG. 1. Comparison of percentage of time spent feeding and alert by broods of Emperor Geese during 1985–1986 (Laing 1991) and 1993–1996 (this study). Vertical bars are 95% confidence intervals for the estimated mean percentages.

TABLE 2. Comparison among goose species in relative amount of time spent in *C. ramenskii* versus *C. subspathacea* habitats, and time feeding in these habitats, by Emperor Geese, Cackling Canada Geese, and Black Brant during 1994–1996 on the Yukon–Kuskokwim Delta, Alaska, as discerned from systematic counts. Within each species, only nonzero counts were included. Habitat and behavior was assessed instantaneously according to the categories detailed in the text. Whole broods were the sampling units with the majority habitat and behavior category for a brood being recorded.

	Emperor Geese ( <i>n</i> = 777)	Cackling Canada Geese ( <i>n</i> = 468)	Black Brant ( <i>n</i> = 190)
Percent of time in <i>C. subspathacea</i>	65	66	81
Percent of time feeding while in <i>C. subspathacea</i>	81	72	72
Percent of time in <i>C. ramenskii</i>	35	34	18
Percent of time feeding while in <i>C. ramenskii</i>	47	56	28

consistently in the plots around blinds than the other two species. That explains why, on average, the abundance of Cackling Canada Geese and Emperor Geese was equal (the mean ratio of 1.02), yet many more counts of  $\geq 1$  broods were obtained for Emperor Geese than other geese (Table 2).

*Effects of habitat and date on behavior.*—Habitat strongly affected behavior of Emperor Goose broods (included as a factor in the parsimoni-

ous ANCOVA model for each age–sex class and behavior). When in *C. subspathacea* habitat, goslings, adult females, and adult males spent 75, 71, and 46% of their time feeding, whereas they respectively spent 42, 34, and 26% of time feeding when in *C. ramenskii* habitat (Fig. 2). Goslings spent more total time (78%) in *C. subspathacea* habitat than did their parents (64 and 62% for females and males). The relative use of *C. subspathacea* versus *C. ramenskii* habitat did not

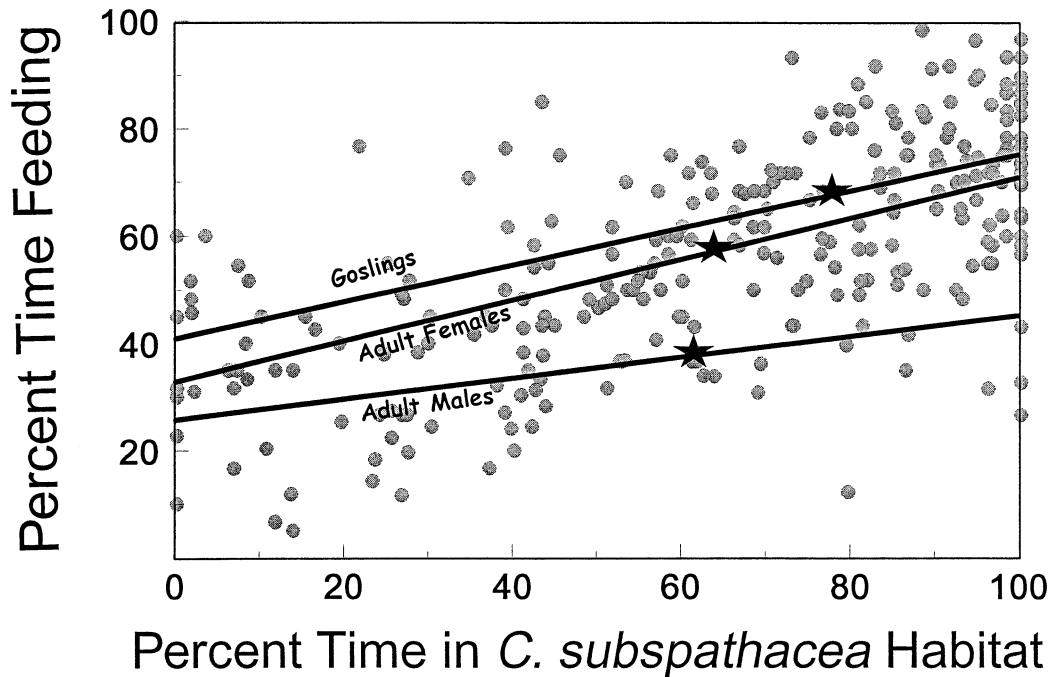


FIG. 2. Percent of time that broods fed in *C. subspathacea* habitat. Raw data shown just for adult females. Lines for goslings, adult females, and adult males were derived from parameters from the parsimonious regression models that also considered the effects of date and goose population density. Stars represent the mean time in *C. subspathacea* habitat for each age–sex class. Left and right intercepts respectively reflect the amount of time spent feeding while in *C. ramenskii* and *C. subspathacea* habitats.

markedly change as the season progressed (models with a date effect were 0.6 to 1.3 AIC units greater than models without a date effect). However, amount of time spent feeding increased with date. Coefficients for goslings, adult females, and adult males were, respectively,  $\beta_{\text{date}} = 0.53$  (SE = 0.19),  $\beta_{\text{date}} = 0.18$  (SE = 0.13), and  $\beta_{\text{date}} = 0.28$  (SE = 0.13). Amount of time on alert did not increase with date for either adult males or adult females.

*Effects of goose density on behavior.*—Goose density affected behavior of goose broods, but the pattern varied among the three age and sex classes. For feeding behavior of goslings, the best model included total goose density of all three species combined, although a model with the combined density of Emperor Geese and Cackling Canada Geese fit nearly as well (Table 3). The poor fit of the other two models demonstrates that there was a strong interspecific density effect on gosling feeding behavior. For adult females, the model with combined density of Emperor Geese and Cackling Canada Geese best described feeding behavior, thus also evidence for interspecific effects. In contrast to gosling and adult females, time spent feeding by adult males was related to intraspecific densities rather than interspecific densities (Table 3). Across the ranges of goose density observed at blinds, time spent feeding by goslings, adult females, and adult males varied positively by an absolute amount of 12, 13, and 16%, respectively. Density effects were similar for time spent on alert—an interspecific density effect for adult females but an intraspecific density effect for adult males (Table 3). Goslings spent virtually no time on alert (Table 1), and thus we did not include them in analyses of alert behavior.

Adding a gull or aircraft disturbance term to the parsimonious models describing adult feeding behavior did not result in lower AIC for either males or females. Similarly, adding gull or aircraft disturbance terms did not result in better models of alert behavior of adult males. For alert behavior of adult females, adding a gull disturbance term to the best model did not lower the AIC value, but an aircraft disturbance term did ( $\Delta\text{AIC} = -1.2$ ). The negative effect of aircraft disturbance on alert behavior of adult females ( $\beta_{\text{alert}} = -3.4\%$ , SE = 1.9) was opposite of what we predicted. During 1994–1996, the percentage of time budget samples

TABLE 3. Values of the Akaike information criterion (AIC; Burnham and Anderson 1998) and AIC weights from models describing time spent feeding and alert by broods of Emperor Goose relative to intraspecific and interspecific densities of geese near observation blinds. Comparison of AIC values among the four competing models constitute the test for density effects on behavior. The lowest AIC value in each column identifies the best model. Parameter estimates are from the best fitting model.

Density term in ANCOVA model	Feeding						Alert			
	Goslings			Adult females			Adult males			
	AIC	weight	AIC	AIC	weight	AIC	AIC	weight	AIC	weight
Null model (no density term)	2.8	0.10	5.5	0.04	0.04	10.0	0.01	0.01	3.8	0.08
Emperor Goose	2.5	0.12	2.9	0.16	0	0	0.95	0.19	2.1	0
Emperor Goose + Cackling Canada Goose	0.4	0.35	0	0.67	5.2	5.2	0.02	0.55	0	0.06
Emperor Goose + Cackling Canada Goose + Black Brant	0	0.43	3.2	0.13	5.8	5.8	0.02	0.18	2.3	5.8
$\beta_{\text{density}}$ (SE)	0.63 (0.31)		0.54 (0.21)		0.94 (0.35)			−0.29 (0.01)	−0.11 (0.02)	



TABLE 4. Values of the Akaike information criterion (AIC; Burnham and Anderson 1998) and AIC weights from linear regression models describing body mass of six-week old Emperor Goose Goslings during 1994–1996.

Variables in model	Females		Males	
	AIC	AIC weight	AIC	AIC weight
None (null model)	0.4	0.21	8.9	0.01
Year	1.3	0.14	9.6	0.01
Density of Emperor Geese	0.7	0.19	9.1	0.01
Density of Emperor Geese + Cackling Canada Geese	0	0.27	5.0	0.07
Density of Emperor Geese + Cackling Canada Geese + Black Brant	0.7	0.19	0	0.90

with gull, aircraft, or fox disturbances was 15, 13, and 2%, respectively.

Aggressive interactions among broods were observed in 24.5% of behavior samples ( $n = 420$ ). Some observers did not record what goose species interacted with a given focal Emperor Goose brood. For the subset of data where species-specific interactions were recorded ( $n = 46$ ), 50% were interspecific interactions.

*Gosling body mass and local goose density.*—Interspecific densities of geese best explained 1994–1996 variation in body mass for both female and male goslings, although the evidence for males was stronger than for females (Table 4). Body mass in those three years was negatively related to total brood densities (Fig. 3). Mean body mass of females and males in those three years was 23.4 and 23.8% less than in 1990. In 1990, we found 89 Emperor Goose nests, 98 Cackling Canada Goose nests, and 56 Greater White-fronted Goose nests. In those same plots in 1997, we found 46, 339, and 93 nests of these respective species, plus 15 Black Brant nests.

*Grazing effects.*—Plots excluded from grazing for 30 days of the brood-rearing period had more than 4× the biomass of *C. subspathacea* as those that were grazed during that same time (Fig. 4). The biomass of grazed plots at 30 days was similar to biomass in plots sampled at the beginning of brood rearing. Therefore, most above-ground primary production of that preferred plant was consumed by geese.

#### DISCUSSION

*Interspecific competition among goslings.*—Goose density clearly affected behavior of Emperor Goose broods and was related to size attained by growing goslings. We invoke intra-

and interspecific competition among geese for food plants as the mechanism causing those observed patterns. There are three reasons why data for goslings are particularly compelling and demographically important. First, goslings have simplistic time budgets focused almost exclusively on food; most time is spent feeding, and the remainder spent resting and digesting, or moving to the next food patch (Table 1; Sedinger et al. 1995b, Fowler and Ely 1997). Unlike adults, goslings rarely interrupt feeding to scan for predators. Thus, a direct relation between food availability and feeding behavior is expected for goslings. Second, food limitation was suggested by the observation that the majority (>80%) of above-ground primary productivity of *C. subspathacea* was consumed by geese. That plant is preferred by feeding Emperor Geese (Laing and Raveling 1993, Schmutz 2001), higher in nitrogen content than nearby meadows of *C. ramenskii* (Ruess et al. 1997, Person et al. 1998), and many studies have demonstrated that limitation of the quantity or nutritive content of food plants strongly affects growth and survival of goslings (Lindholm et al. 1994, Gadallah and Jefferies 1995, Sedinger et al. 1997). Third, body mass of six-week old Emperor Goose goslings was a function of interspecific goose densities, and gosling body mass is a strong predictor of subsequent survival (Schmutz 1993, Sedinger et al. 1995a). Demonstration of interspecific competition requires evidence of shared use of resources, a limitation of resources, and a demographic consequence (Wiens 1989). Our data meet those criteria and support the conclusion that demography of juvenile Emperor Geese is affected by competition with other goose species.

*Differences among ages and sexes in effects of goose density.*—For both goslings and adult fe-

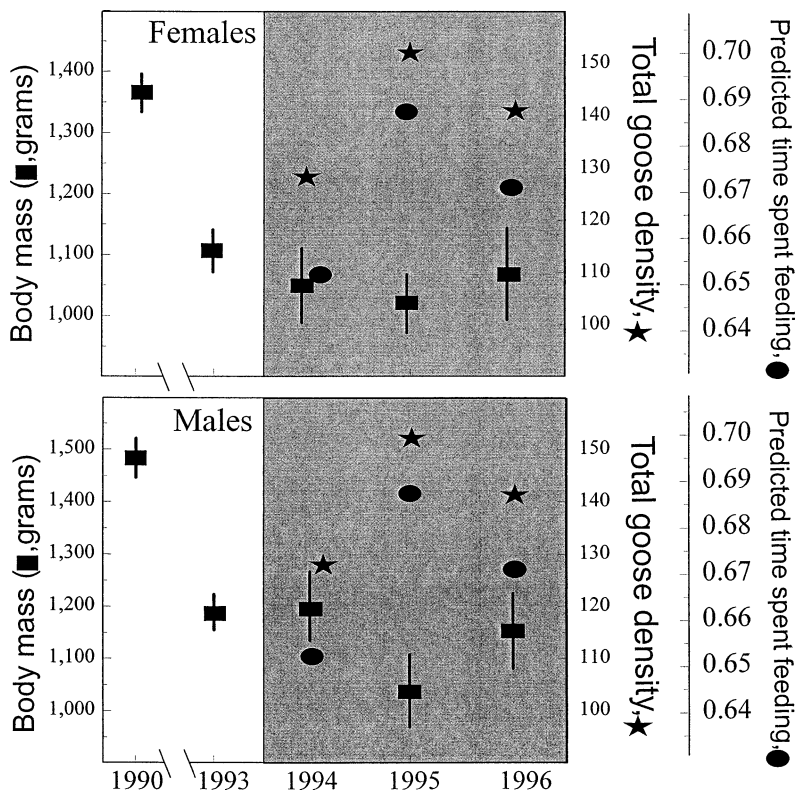


FIG. 3. Body mass (means and 95% confidence intervals) of Emperor Goose goslings at approximately six weeks of age. The shaded areas (1994–1996) depict the inverse relation between body mass and brood densities of all goose species (see Table 4), as well as the predicted time spent feeding by goslings, as calculated from the parsimonious regression model in Table 3.

males, time spent feeding by Emperor Geese was related to interspecific goose densities. However, the best-fitting model for those two groups differed—both models included Cackling Canada Goose density but only the model for goslings also included density of Black Brant. These results are consistent with the findings that Emperor Goose goslings spent more time in *C. subspathacea* versus *C. ramenskii* habitats than their parents, and that Black Brant spent disproportionate amounts of time in *C. subspathacea* habitats relative to other species.

The greater use of *C. subspathacea* by Emperor Goose goslings than by their parents may have been caused by multiple factors. *Carex subspathacea* is less abundant but with higher nitrogen content than *C. ramenskii* (Laing and Raveling 1993, Ruess et al. 1997, Person et al. 1998). Because of their small size and demands for growth, goslings need to consume less absolute

amounts of food but food of higher nutritional content (higher nitrogen for protein synthesis or less fiber to enhance digestibility; Demment and Van Soest 1985, Sedinger 1997). Thus, one hypothesis is that parents may more ably subsist on *C. ramenskii* than goslings. That rationale could also apply to the disproportionate use of *C. subspathacea* by Black Brant, because Black Brant are the smallest of the four goose species breeding on the Yukon–Kuskokwim Delta.

Adult males differed from females and goslings in that their feeding and alert behavior was related only to conspecific densities. Male geese are generally less nutritionally taxed during egg laying and incubation (Ankney 1977, Ankney and MacInnes 1978) and thus would be expected to begin the brood rearing-period with less need to feed. We suggest that the behavioral response to goose density in males was primarily alert behavior, and that relation-

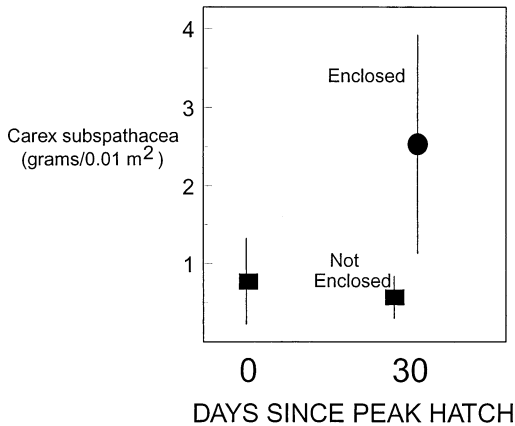


FIG. 4. Biomass of *C. subspathacea* in eight sets of three types of 0.1 m<sup>2</sup> plots. The three plot treatments were as follows: sampled at peak hatch of goslings and representing initial biomass at start of brood rearing, sampled at 30 days after peak hatch and always available to be grazed (not enclosed) by broods, and sampled at 30 days after peak hatch and enclosed within a wire mesh fence for those 30 days and thus unavailable to grazing. Symbols represent means and vertical bars represent 95% confidence intervals.

ships between feeding and density were simply correlated responses. Further, we speculate that the lesser rates of alert behavior with greater densities of Emperor Geese were a consequence of a selfish-herd effect (Hamilton 1971), wherein the costs of alert behavior are shared among unrelated members of a group (i.e. other broods) and from which one would predict that time spent alert would be inversely related to the number of broods. During non-breeding seasons, positive relationships between flock size and time spent feeding by Emperor Geese (Schmutz 1994) and other geese (Lazarus 1978) support that hypothesis. The intraspecific nature of that density effect may be because Emperor Geese were more consistently around blinds and other Emperor Geese, whereas Cackling Canada Geese and Black Brant were more transient (as indicated by CV of counts).

*Change in strength of competition over time.*—Comparison of our behavior data to that obtained in 1985–1986 and our body-mass and density data from 1993–1997 to that from 1990 suggests that interspecific competition among broods is a recent phenomenon, and likely corresponds with the recent rapid increase in

abundance of Cackling Canada Geese (Bowman et al. 1997). All three age–sex classes of Emperor Geese showed greater time spent feeding during 1993–1996 than observed in Laing's (1991) Yukon–Kuskokwim Delta study in 1985–1986 (Fig. 1). Laing's (1991) study occurred at Kokechik Bay, ~50 km north of our Manokinak River site. Although the array of available plant communities at each site appeared similar, there may have been some inherent differences among study sites that led to these differing results. However, at a site between the Manokinak River and Kokechik Bay, Fowler and Ely (1997) similarly observed that time spent feeding by Cackling Canada Geese increased with recent increases in their density. Further, patterns of change in densities of geese at Manokinak River and Kokechik Bay were each generally similar to the overall pattern of change observed on the Yukon–Kuskokwim Delta (Bowman et al. 1999; this study; U.S. Fish and Wildlife Service unpubl. data). Laing (1991) observed very few Cackling Canada Geese during her observations of Emperor Goose broods, whereas we commonly observed aggressive interactions among species, with the frequency of interactions among broods approximately equal that seen in a Lesser Snow Goose population (Mulder et al. 1995) where competition for food was great and survival of juveniles declined precipitously (Cooke et al. 1995).

The large difference in body mass of Emperor Goose goslings in 1990 versus those captured in later years mirrors changes in Cackling Canada Geese for which a progressive decline in body mass of known-age goslings was documented and equated to an approximately 20% reduction in size at fledging (C. Ely unpubl. data). The recent decline in the fall age ratios of Emperor Geese, as assessed annually by aerial photographic surveys (U.S. Fish and Wildlife Service unpubl. data) suggests a recent decline in postfledging survival of juveniles, as would be expected with reduced gosling body mass.

We observed interspecific competition among broods of geese despite concurrent documentation of clear species-specific preferences for brood habitats (Schmutz 2001). We suspect that the *C. ramenskii* and *C. subspathacea* habitats preferred by Emperor Geese probably received little use by Cackling Canada Geese prior to the

recent dramatic increase in their abundance. A shift in habitat use of Cackling Canada Geese (towards more use of *C. ramenskii* and *C. subspathacea*) with their increasing densities is consistent with an ideal free distribution model (Fretwell and Lucas 1970), which predicts that less preferred habitats become equally valuable as densities rise in the most preferred habitats (Vickery et al. 1995).

*Causes for density changes and prognosis for the future.*—The recent increase in densities of Cackling Canada and Greater White-fronted geese on the Yukon–Kuskokwim Delta is not likely due to increases in recruitment rates, especially given the evidence for negative effects of density on growth of Cackling Canada Goose goslings. It is highly probable that those population increases have occurred due to changes in adult survival rates. Perturbations of adult survival are expected to have proportionally much greater effects on population growth than comparable changes to recruitment (Schmutz et al. 1997), and harvest of adult geese has been perturbed (Raveling 1984, Sedinger 1996a). Legal harvest of Cackling Canada Geese was prohibited for much of the 1980s and 1990s (Sedinger 1996a), and survival rates apparently increased over that time (Raveling et al. 1992; U.S. Fish and Wildlife Service unpubl. data).

The demography and anthropogenic perturbation of goose populations when they are allopatric clearly influence competitive interactions during the seasons they are sympatric. Cackling Canada Geese may not out-compete Emperor Geese per se, but rather increases in their density may negatively affect gosling growth and recruitment for both species. Population increases for Cackling Canada Geese may continue until the reduction in their recruitment is sufficient to counteract the increase to their adult survival. Given that there is no evidence that adult survival rates of Emperor Geese have substantially changed over time (Petersen 1992, Schmutz et al. 1994, Schmutz and Morse 2000), reductions in recruitment due to interspecific competition may cause declines in their population growth rate. The recent decline in their fall age ratio appears symptomatic of reduced recruitment. Negative effects of goose density on recruitment implies that population growth rate of Emperor Geese will only increase if interspecific competition is

reduced or adult survival rates are increased. The potential for positive effects of goose density on plant nutrition and subsequent gosling growth (Person 2001) and survival, which may arise through a herbivore–plant optimization process (Hik and Jefferies 1990), needs to be investigated.

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